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LIMNOPHILA CERATOPHYLLOIDES AND *L. FLUVIATILIS* TWO HETEROMORPHIC AFRICAN SPECIES

by A. Raynal & D. Philcox

Résumé : *L. fluviatilis* A. Chev., espèce méconnue, est distinguée de *L. ceratophylloides* (Hiern) Skan avec laquelle elle avait été confondue, et introduite dans la clef de détermination des espèces publiées par Philcox (1970); les auteurs donnent la description et la répartition géographique de ces deux espèces. En outre, ils tentent de circonscrire la variation morphologique de ces plantes qui croissent et fleurissent soit dans l'eau soit sur la vase émergée, et où on observe divers aspects d'une forte hétéromorphie (hétérophyllie, cléistogamie, etc.).

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Since publication of the revision of the genus *Limnophila* (D. Philcox, Kew Bull. **24** (1) : 101-170, 1970) the authors are now agreed that the concept of *L. ceratophylloides* (Hiern) Skan shown in that work contains two distinct elements. Hitherto the two species which Philcox considered to make up *L. ceratophylloides* were the East African plant bearing that name and the West African *L. fluviatilis* A. Chev. On closer subsequent investigation however it was noticed that although the plants studied towards this species concept at first appeared to show a similar heteromorphism, they also differed in floral characters as well as in their ecology.

The two species comprising this complex are very plastic but at the same time very similar in habit and appearance. Within the genus *Limnophila*, both are among the species displaying a wider ecological range and an accordingly greater morphological variation. They may grow as:

1 - water plants bearing submerged cleistogamous flowers and fruits;
2 - aerial-flowering aquatics with the upper part of the submerged stems standing above water. The same stem may bear differently shaped leaves and flowers varying from cleistogamous to more or less chasmogamous;
3 - plants creeping on mud with entirely aerial and chasmogamous flowering.

Thus a single species may occur in roughly three distinct habits, with each example having its own distinctive flower and fruit characters. The standard approach clearly fails to distinguish properly the taxonomic entities and it is agreed that taxonomic boundaries are far from obvious, especially when studied on herbarium specimens. To some extent, delimitations of such groups may not respond to usual taxonomic methods hence we had to try somewhat unusual approaches, both morphological and biological, with the hope that they would clarify that difficult taxonomy.

From both field and herbarium observations, it became obvious that :

1 - the same species could have very different appearances;

2 - different species could display parallel variations, so that two different species in the same biological state are looking much closer to each other than two extremes of the biological variation within a single species.

We hope to point out noticeable characters observed in the species discussed here and from our findings we shall try to analyze the morphological variation shared by the different species, and to extract the taxonomic bond tying the extreme ecological forms.

MORPHOLOGICAL REMARKS.

GENERAL HABIT.

The species we are considering are aquatic plants growing in shallow water and rooting in the mud. The stems, erect and floating in water, may be entirely submerged if the water is deep enough and the plants are then growing in the same way as *Ceratophyllum* or *Najas*. In that condition they may carry out a complete biological cycle, bearing flowers and fruits, without any aerial phase.

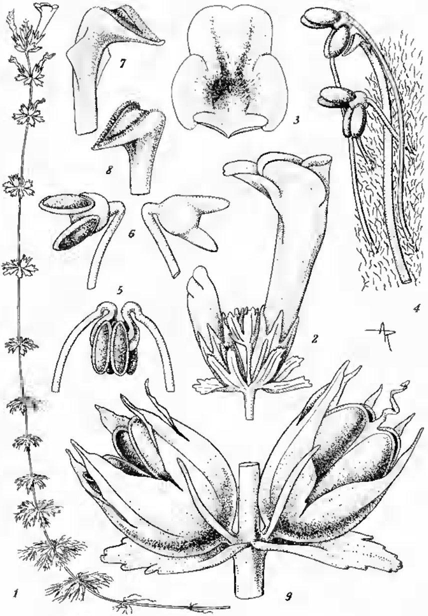
If the water is shallower the stems may grow through the surface and the plants then have the habit of *Myriophyllum* or *Hippuris*. A noteworthy and gradual variation of the leaves and flowers takes place as the stems become aerial.

When growing in temporary water, these *Limnophila* first produce submerged stems during the flood season and when the water recedes, the stems, prostrate on the wet mud, root at the nodes and then act as a kind of rhizome on which the leaves quickly decay. From each rooting node erect shoots arise which may eventually separate into independent plants. Living terrestrially such plants do not retain any of the features characterising the submerged form of the original stock.

LEAF SHAPE.

Obvious heterophylly is to be seen in these species. Most aerial leaves are sessile, opposite, decussate along the stem, 3-5-parallel-nerved and the margin more or less deeply toothed, at least towards the apex. Each of them has an axillary bud which developes into either a flower or a shoot.

Most submerged leaves are deeply dissected and have long linear segments in apparent whorls of 6-8 (generally) at the nodes. They look verticillate but it must be noticed that only two axillary buds occur at each



Pl. 1. — **Limnophila ceratophylloides** (Hiern) Skan, aerial plant: **1,** flowering stem, lower part submerged × 1; **2,** chasmogamous flower and bud × 5; **3,** corolla seen from above × 5; **4,** stamens and style inside the corolla tube × 20; **5,** one pair of stamens adhering to each other by the fleshy connectives × 30; **6,** anther front and back view × 30; **7,** top of style bearing two lateral processes below the stigma × 30; **8,** another one, without processes × 30; **9,** fruits from chasmogamous flowers × 10 (**1-3, 5, 6, 8** and **9** drawn after *J. & A. Raynal* 12163; **4** and **7,** after *Wild* 1078).

Source : MNHN, Paris

node, these buds being opposite and decussate along the submerged stems as they are along the aerial ones.

Between these two extreme leaf shapes all intermediates are to be observed. On amphibious stems, the appearance of the leaves changes from one node to the next. The verticillate elements seem to join together towards two " poles " fronting the axillary buds and upwards along the stem, there is a progression towards opposite leaves, by coalescence. The first opposite leaves are fan-shaped, deeply palmately dissected and become, on the next upper nodes, less and less dissected and finally reach the ovate toothed outline.

We may consider that the whole foliar arrangement is opposite-decussate on both aerial and submerged stems. On underwater shoots it is concealed by the splitting of a single leaf into several pieces, each one looking like a leaf. These submerged elementary leaf pieces correspond to the main nerves, arising directly from the insertion of aerial simple leaves. The palmately-nerved emerged leaf-blade is equivalent to a set of submerged elements, as numerous as the nerves in the aerial leaf, and regularly distributed on half the girth of the stem. Surrounding a submerged node is a verticil of foliar elements, but only two leaves and two buds.

It is to be noted that another path towards heterophylly seems to occur in other groups of *Limnophila*. In some sections (*Integrifoliex, Striatæ*, see PHILCOX, *l.c.*, p. 107-108), the aerial leaves are pinnately nerved instead of palmately and when dissected submerged leaves are produced, they are deeply pinnately cut and arranged in the same way as the aerial ones. Dissected or not, each one relates to an axillary bud and they may be either opposite or verticillate all along the amphibious stem. To each type of aerial leaf there corresponds a submerged one. While the shape of the blade is modified, the leaf keeps its morphological unity and does not split from its base into several independent similar elements. It seems that only palmately nerved leaves can split so deeply that they seem to lose their morphological unity.

With this in mind, one is able to consider this difference in heterophylly as enhancing PHILCOX's definition of sections: extreme heterophylly, in which the foliar entity is no longer evident even from its very base, seems characteristic of sect. *Limnophila*.

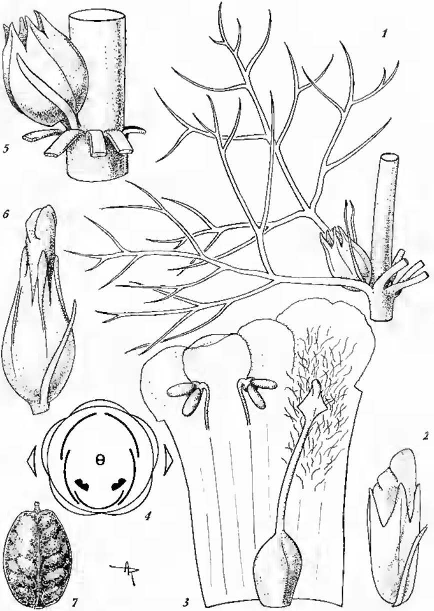
INFLORESCENCE.

The flowers are solitary in the axils of the leaves, except on some aerial shoots of *L. fluviatilis* where they may be grouped on very short, few-flowered, axillary racemes.

On submerged stems, a single flower occurs at every flowering node: one of the two axillary buds does not develope.

On aerial stems, the two axillary buds generally developed and each node bears either two opposite flowers (or axillary flowering racemes)

Source : MNHN, Paris



Pl. 2. — **L. ceratophylloides** (Hiern) Skan, submerged plant: **1,** node bearing dissected leaves and one fruit × 5; **2,** cleistogamous flower × 10; **3,** cleistogamous corolla laid open showing stamens and gynaecium × 20; **4,** diagram of a cleistogamous flower; **5,** fruiting calyx × 10; **6,** young fruit, the hooded corolla remaining on its top × 10; **7,** capsule from a cleistogamous flower × 10. (Drawn after *Thollon 204.*)

or one axillary shoot one and flower (or axillary flowering raceme). The two opposite flowers borne on an aerial node do not appear at the same time, one developing earlier that the other; as a consequence, these two flowers, when observed in the field as well as on herbarium specimens, are at different biological stages, one being at anthesis as the second is still in bud.

We can consider that one of the two buds is promoted with regard to the other; on a submerged node, the " promoted " bud developes a flower and the other remains inhibited; on an aerial node, it produces the early flower, the " non-promoted " bud giving the later one.

From one node to the next above it the " promoted " buds along the stem are describing either a spiral line or a zigzag one; this line turns through ninety degrees from one node to the next and always turns in the same direction, the spiral rotation being either clockwise or not. The zigzag sequence results from reversing the rotation at every node.

FLOWERS.

The typical flowers, aerial and chasmogamous, look very different from the reduced, submerged, cleistogamous ones; in some cases, slightly reduced flowers, of an intermediate kind, occur along the transitory segment of the stem going from submergence to emergence.

Bracteoles and calyx are nearly always dotted with small sessile golden glands; glabrous when submerged, they may vary from shortly pubescent to coarsely or laxly long white patent-hirsute when aerial.

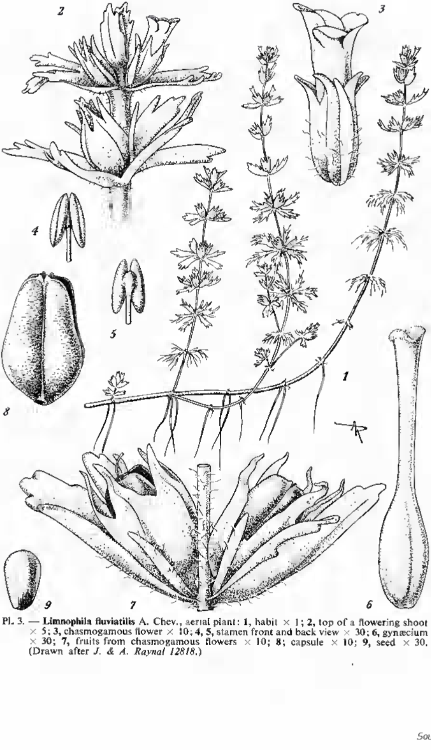
The corolla, long-tubed with expanded lobes in chasmogamous flowers, is much smaller in cleistogamous ones, the lobes remaining closely imbricate, making a hood clasping the sexual parts. Its size is more or less reduced, the whole flower may be fairly small on completely submerged stems, but its size may be gradually larger on the transition zone of emerging stems. While such flowers are still cleistogamous, their morphological features however gradually vary towards those of open aerial flowers.

The stamens of chasmogamous flowers are typically in two pairs, the anterior one with longer filaments than the posterior ones; the anthers, grouped (or even adhering) by pairs, are all together around the stigma, topping an elongate style, beneath the upper lip.

In cleistogamous flowers, the filaments are very short and generally equal in length; the four anthers are then standing above the ovary and clasping the very short style. In *L. ceratophylloides*, not only the size, but the number of stamens itself, may be reduced. With the posterior pair being absent, the floral diagram of cleistogamous flowers looks quite different from that of the genus, and even of the tribe containing *Limnophila*.

DISCRIMINATION BETWEEN *L. CERATOPHYLLOIDES* AND *L. FLUVIATILIS*.

As has been shown, the general habits of the two species are very similar. However, there are major differences when the flowers are studied



Pl. 3. — **Limnophila fluviatilis** A. Chev., aerial plant: **1,** habit × 1; **2,** top of a flowering shoot × 5; **3,** chasmogamous flower × 10; **4, 5,** stamen front and back view × 30; **6,** gynæcium × 30; **7,** fruits from chasmogamous flowers × 10; **8**; capsule × 10; **9,** seed × 30. (Drawn after *J. & A. Raynal 12818.*)

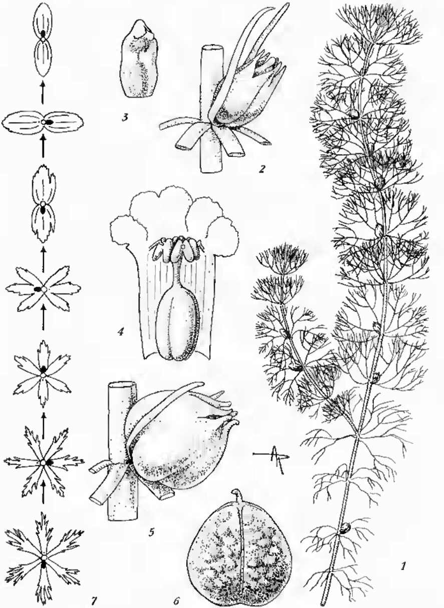
microscopically. Flowers borne on the emerged stems of *L. ceratophylloides* are quite large, from 10 to 12 mm long, and are moderately to densely villous within the tube mainly on the posterior side. Aerial flowers of *L. fluviatilis* are much smaller, 4-5 mm long, and generally glabrous within the tube. This alone is not enough to warrant specific separation but further clear distinction is shown by the stamens. In both types of flowers of *L. fluviatilis* the number of fertile stamens is constantly four and the anthers have two more or less parallel thecæ which are borne on the ends of the filament attached approximately at the middle by the slightly swollen connective. In *L. ceratophylloides* the chasmogamous flowers have four fertile stamens while the cleistogamous flowers have generally the stamens reduced to the anterior pair only. Here in both types of flowers the attachment of the anthers differs from that in *L. fluviatilis*. In *L. ceratophylloides* the anthers do not have a median attachment with the filaments but are attached by one of their poles to the greatly swollen connective with the thecæ divergent instead of being subparallel. In *L. fluviatilis*, the papillose stigma is nothing but the truncate apex of the style; in *L. ceratophylloides* it is more complex, the two narrowly triangular lobes, appressed one to the other, abruptly bending, are making a hook at the top of the style. It seems that the two " processes " widening the style just below the stigma are inconsistent; they may be small or absent without any further difference between the specimens.

These characters together are considered good enough reason for a clear taxonomic distinction. There are however several other minor characters which appear to be constant and still add weight to the argument of separation. For example, fruits from the cleistogamous flowers of *L. fluviatilis* are very pale brown in colour, almost translucent and more or less spherical in shape while those of *L. ceratophylloides* are dark brown and not at all translucent; also like those of the chasmogamous flowers they are not spherical but ovoid truncate-emarginate.

The above separation of the two species from PHILCOX's original concept now necessitates a structural revision of that part of his key to the species of *Limnophila* used to distinguish *L. ceratophylloides* (Kew Bull. **24 (1)** : 108-109). The following should serve to differentiate them both either from specimens with or without submerged stems:

1. Finely divided submerged leaves present:
    4. Bracteoles 1,5-9 mm long:
        4a. Stamens of chasmogamous flowers 4, cleistogamous flowers 2 only; anther thecae divergent, attached by end to greatly inflated filament connective; hooked stigma; fruits from cleistogamous flowers dark brown, opaque, ovoid truncate-emarginate.......... 5. *L. ceratophylloides.*
        4a. Stamens 4; anther thecae subparallel, median attached to slightly swollen filament connective; truncate stigma; fruits from cleistogamous flowers pale brown, translucent, subspherical.... 5a. *L. fluviatilis.*

1. Finely divided submerged leaves absent:
        22. Bracteoles 1,5-9 mm long:
            22a. Corolla 10-12 mm long, tube villous within; anther thecæ divergent, attached by end to greatly inflated filament connective.............................. 5. *L. ceratophylloides.*



Pl. 4. — **L. fluviatilis A.** Chev. submergedplant: **1,** submerged flowering stem × 1; **2,** cleistogamous flower × 10; **3,** corolla × 10; **4,** cleistogamous corolla laid open, showing the four anthers clasping the stigma × 20; **5,** fruiting calyx from a cleistogamous flower × 10; **6,** capsule × 10; **7,** heterophylly along an amphibious stem, lower part submerged, upper one aerial: leaf pairs on successive nodes × 1; the large black dot symbolizes the only —or early— bud to develope. **(1-6,** drawn after *Letouzey 7252*; **7,** after *J. & A. Raynal 12818, in vivo.*)

22a. Corolla 4-5 mm long, tube glabrous to subglabrous within; anther thecæ subparallel, median attached to slightly swollen filament connective.................... *5a. L. fluviatilis.*

In the course of this study type material of *Ambulia baumii* Engl. & Gilg was further studied and proved to match the type specimen of *L. ceratophylloides.*

5. L. **ceratophylloides** (Hiern) Skan

in Dyer, Fl. Trop. Afr. 4 (2) : 317 (1906); Eyles *in* Trans. Roy. Soc. S. Afr. 5 : 472 (1916); Peter, Wasserpfl. Deutsch. Öst.-Afr. : 127 (1928); Philcox, Kew Bull. 24 (1) : 122 (1970), *p.p.*

— *Stemodiacra ceratophylloides* Hiern, Cat. Afr. Pl. Welw. 1 : 759 (1898). — Type : *Welwitsch 5778*, Angola, Huilla (BM, holo-, K, iso-).

— *Stemodia ceratophylloides* (Hiern) K. Schum. *in* Just, Jahresber. 26 (1) : 395 (1900).

— *Ambulia ceratophylloides* (Hiern) Engl. & Gilg *in* Warb., Kunene- Sam. Exped. : 362 (1903).

— *Ambulia baumii* Engl. & Gilg, *loc. cit.* : 361. — Type : *Baum 750*, Angola, (BM K, iso-).

— *Stemodiacra sessiliflora* auct. *non* (Vahl) Hiern : Hiern, *loc. cit.* : 758, *quoad pl. afric. non Hottonia sessiliflora* Vahl 1791.

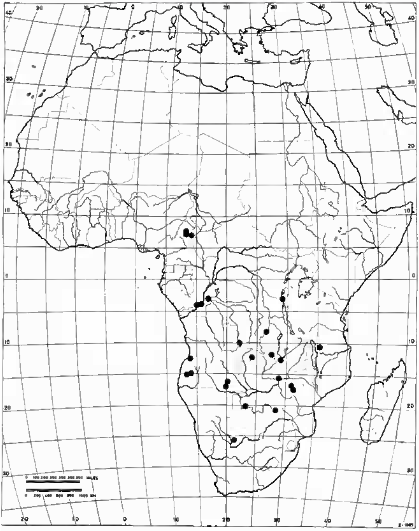
Amphibious perennial. Stems: aerial stems to 20 cm tall, simple or branching, glabrous to laxly white hirsute or covered lightly with small sessile yellow glands; submerged stems to 60 cm long, simple or branching, glabrous. Leaves on aerial stems verticillate to opposite, irregularly pinnatisect to lacerate, 5-8 × 1-2 mm, densely punctate, glabrous, hirsute or yellow-glandular; submerged leaves to 2,5 cm long, pinnatisect-multifid, segments capillary or more usually flattened, glabrous. Flowers solitary axillary, sessile, cleistogamous flowers present on submerged stems. Chasmogamous flowers: bracteoles 1,5-4 mm long, narrowly linear, glabrous to very shortly hirsute; calyx 3-5 mm long, glabrous or hirsute, yellow-glandular; corolla 6-10 mm long, mauve to lilac with darker throat, externally glabrous, densely villous within the tube mainly on the posticous side; stamens 4 with contiguous anthers at anthesis, filaments 0,75-3 mm long, anthers attached by one pole to largely inflated connective, thecæ divergent; stigma unequally bilobed with one lobe somewhat extended, narrowly deltoid, perpendicular to the style, style 1-4 mm long; Capsule 2,5-3,5 mm long, dark brown, emarginate, broadly ovoid. Cleistogamous flowers: bracteoles 2,5-4 mm long, narrowly linear, glabrous; calyx 3-3,5 mm long, glabrous; corolla 3,5-4 mm long, villous within the tube; stamens generally 2, filaments c. 0,75-1 mm long; style c. 1,5 mm long; capsule 2,5 mm long, dark brown to light brown, opaque, broadly ovoid.

Selection of specimens examined:

Cameroun : *Jacques-Félix 8598*, Ngaoundéré, P; *8881*, 45 km from Ngaoundéré on road to Belel, P; *J. & A. Raynal 12163*, Djouroum, 13 km S of Ngaoundéré, K, P.

Congo Republic: *Thollon 204*, Mpila, Brazzaville, P.

Zaïre : *Breyne 2134*, Menkao, BR; *Symoens 12474*, Kakielo, Katanga, BR; *Vanderyst 1147, 1162*, Wumbali, BR; *Quarré 8071*, Keyberg, BR; *de Witte 4298*, Upemba Nat. Park, BR; *Young 259*, Dilolo, P.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Pl. 5. — Geographical range of **Limnophila ceratophylloides** (Hiern) Skan.

Burundi : *Michel & Reed 1662*, Kimaro, Mosso, BR.

Tanzania : *Milne-Redhead & Taylor 10845*, Songea, BR, K.

Zambia : *Fanshawe 412*, Mwinilunga, BR, K; *Milne-Redhead 3709*, Mwinilunga, BR, K; *West 3541*, Kafue Gorge, K, SRGH.

Rhodesia : *Miller 4411*, Matopo Distr., BR; *Wild 1078*, Cleveland Dam, Salisbury District, K, SRGH; *3831*, Mazoe District, alt. 1200 m., SRGH.

Botswana : *Gibbs Russel & Biegel 1469*, Northern District, Khwai Riv., BR; *Richards 14686*, Northern District, near Maun, Thamalakene Riv., alt. 900 m, K.

Angola : *Welwitsch 5776*, Huila, from Lopollo to Nene and Ohai, BM, C, COI, K, P; *5778*, between Lopollo and Humpata, BM, K; *Gossweiler 3858*, Benguella, K; *Baum 750*, Kutue Riv., alt. 1200 m, BM, BR, COI, E, K, M.

South West Africa : *Dinter 7618*, Kanovtey, K, M; *7245*, Niangana to Okavango, BM, K, M.

5a. L. **fluviatilis** A. Chev.

Bull. Mus. Nat. Hist. Nat. Paris, ser. 2, **4** : 587 (1932); A. Raynal, Adansonia **7** (3) : 351 (1967).

Type : *Chevalier 43079*, Mali, Gao (P, holo-).

— *L. fluviatilis* A. Chev. f. *fluviatilis*, *loc. cit.*

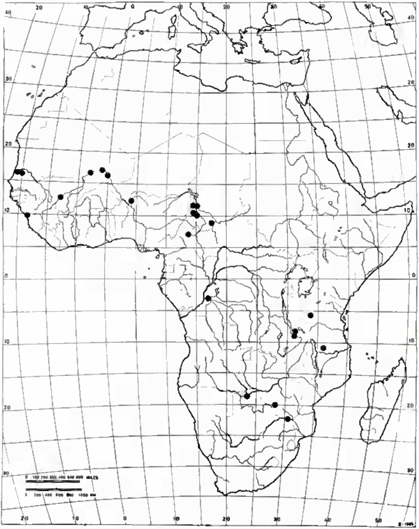
— *L. fluviatilis* A. Chev. f. *terrestris* A. Chev., *loc. cit.*: 588 (1932). — Type : *Chevalier 43766*, Mali, Bourem - Bamba (P, holo-).

Amphibious perennial. Stems: aerialstems to 10 cm tall, simple or rarely branching except at base, glabrous to sparsely hirsute, particularly above; submerged stems to 35 cm long, branching, glabrous. Leaves on aerial stems verticillate, irregularly pinnatisect to lacerate, 4-18 × 1-6 mm, glabrous, densely punctate, frequently with sessile yellow glands; submerged leaves to 2,5 cm long, pinnatisect-multifid, segments capillary or more usually flattened, glabrous. Flowers solitary axillary, sessile on submerged stems, solitary or clustered on very short axillary few-flowered racemes on aerial stems; cleistogamous flowers usually present on submerged stems. Chasmogamous flowers: bracteoles 2-3,5 mm long, narrowly linear, glabrous to sparsely hirsute; calyx 3-4,5 mm long, glabrous, frequently with yellow glands; corolla 4-6,5 mm long, white to lilac, throat yellow, externally glabrous, occasionally very sparsely villous within the tube; stamens 4 with contiguous anthers at anthesis, filaments 0,5-2 mm long, anthers median attached to slightly swollen connective, thecæ subparallel; stigma truncate to emarginate, style 1-2 mm long; capsule 3-4 mm long, dark brown, subtruncate to emarginate, subflattened, ovoid. Cleistogamous flowers; bracteoles 2,5-6 mm long, narrowly linear, glabrous; calyx 3-6 mm long, glabrous; corolla 3,5-4,75 mm long, glabrous to sparsely villous within tube; stamens 4 with contiguous anthers, filaments c. 0,25 mm long, anthers as above; style 0,75-1 mm long; capsule 2,25-4 mm long, light brown, translucent, broadly ovoid, emarginate to subspherical.

Senegal : *Leprieur s.n.*, " in inundatis, désert Sahara ", P; *Perrottet 579*, s.loc., P; *J. & A. Raynal 6640*, Ntiago, P.

Guinea : *Chillou 946*, s. loc., IFAN; *1080*, Friguiagbé, BR, IFAN.

Mali : *Chevalier 43055, 43074, 43079*, Gao, P; *43766, 43766 bis*, Gao to Bourem and Bamba, P; *43825*, Kabara, Bougouberi, P; *J. & A. Raynal 5421*, Katibougou, P;



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Pl. 6. — Geographical range of **Limnophila fluviatilis** A. Chev.

de Wailly 4982, 5021, Gao, P; *5387*, Gao to Kokoromme, P; *Hourst s.n.*, « boucle du Niger », P.

Nigeria : *Vaillant 2785*, Sokoto Prov., Birnin Kebbi, K.

Cameroun : *Hepper 4056*, W side of Riv. Shari, 5 km downstream from Fort Lamy, BR, K; *Letouzey 7168*, Naga, 15 km W from Fort Foureau, P; *7252*, 70 km ENE of Maroua, P; *J. & A. Raynal 12818*, Gandjam, 13 km WNW of Yagoua, P; *13266*, Sadolkoulay, 35 km E of Ngaoundéré, P.

Central African Republic : *Chevalier 8680*, Bahr-el-Azreg, near Fort Archambault, P.

Zaïre : *Laurent 603*, near Bokala, BR.

Tanzania : *Burtt 3704*, Manyoni District, Kazikazi, BR, EA, K; *Milne-Redhead & Taylor 10837*, Songea District, Kwamponjore Valley, c. 9,5 km of Songea, alt. 1000 m, B, BR, EA, K, LI.

Zambia : *Bullock 1093*, Lake Chila outflow, K; *Richards 9930*, Abercorn District, Lumi River, alt. 1680 m, BR, K.

Rhodesia : *Drummond 5761*, Gwanda District, near Chiturupadzi, 40 km NNW of Bubye-Limporo confluence, K, SRGH; *Miller 2394, 4548*, Matobo District, K, SRGH; *4411, ibid.*, BR, K, SRGH.

South West Africa : *de Winter & Marais 4874*, Okavango Territory, K, M; *5029*, Kapako Camp, c. 6 km W of Mupini Mission Station, K, M.

GEOGRAPHY AND ECOLOGY.

The overall distribution of *Limnophila fluviatilis* and *L. ceratophylloides* is quite different although these species to some extent overlap. However, if they do both occur in the same general region, they do not occur in the same place: their different ecological requirements help to separate the two species biologically.

L. fluviatilis occurs mainly in the dry savanna zone surrounding the wet " guineo-congolan " region from Senegal to South West Africa. Its occurrence in the Congo basin is connected with the ecology of a large stream valley, and at the same time with local climatic conditions. It grows in river beds and their depending marshes and ponds where soil is seasonally inundated by a stream flood; water level may vary greatly throughout the year, and, when the water level drops and the soil becomes exposed, the vegetation is sparse enough to leave bare patches where the *Limnophila* may develope.

The range of *L. ceratophylloides* corresponds to a wetter climatic area, extending around the rain-forest and through the zone of " sudano-zambesian " dry forest, from Cameroun to South West Africa. It is noticeable that the plant seems not to occur westwards from Cameroun, though suitable ecological conditions occur as far as Guinea and even Senegal. This species grows in grassy marshes seasonally or permanently flooded by raising edaphic water or rain water. It seems that this species generally does not grow in marshes transgressed by stream waters.

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